

Can navigation locks be used to help migratory fishes with poor swimming performance pass tidal barrages? A test with lampreys



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ABSTRACT

Worldwide, tidal barrages reduce aquatic habitat connectivity and limit fish movements, especially for diadromous migrating species. Providing fish passage at these structures is crucial but technically and economically challenging. We measured the performance of a navigation lock, employed as a single-chamber vertical-slot fish pass, at a tidal barrage by the mouth of a tributary of the River Ouse, NE England. In autumn 2015, 265 European river lamprey *Lampetra fluviatilis* were tagged with Passive Integrated Transponders (PITs) and released in 11 replicate trials ($n = 157$ in lock, $n = 108$ immediately below lock). Fifty nine lamprey were double tagged with PIT and acoustic tags and released in the Ouse, 350 m downstream of the barrage. The percentage of lamprey attempting to pass the upstream gates during PIT trials was moderate to high (55 and 93% for lamprey released below, and in the lock, respectively). Passage efficiency, for lamprey attempting to pass the upstream gates, was also high (average of 66% for releases in lock, 78% for releases below lock). Ninety percent of lamprey, released below the lock and attempting to migrate upstream passed the entire lock in <128 min following release. However, acoustic-tagged lamprey displayed poor attraction to the lock under prevailing high river-discharge conditions. Overall, 36% of acoustic-tagged lamprey attempted to pass the barrage, mostly comprising lamprey released at low tide (cf. high tide), generating a high passage efficiency of 76% (16/21). However, 15 individuals passed through the sluices and only one used the lock. Nevertheless, using navigation locks as fishways has the potential to provide increased access between estuarine and river habitats for a range of biota, including those with poor swimming performance, but effectiveness is dependent on managing water discharge routes. Future studies using different operating protocols, especially to improve fish attraction under different environmental conditions and for a range of species, are encouraged.

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1. Introduction

Habitat loss is the greatest threat to global biodiversity (Pimm and Raven, 2000) and estuaries provide key migration routes for a range of diadromous and euryhaline fish species (Baras and Lucas, 2001; Buysse et al., 2008). However, rivers and estuaries have been altered worldwide by the construction of anthropogenic structures (Nilsson et al., 2005), which dramatically reduce their longitudinal connectivity and hinder movement of these species between key habitats (Baras and Lucas, 2001). This has caused severe fish

population declines and even population extinctions (Limburg and Waldman, 2009; Lucas and Baras, 2001).

River channel obstacles close to the river mouth or in the estuarine area have the greatest impact on diadromous biota (Kemp and O'Hanley, 2010; Nunn and Cowx, 2012), as they obstruct passage to and from a large part of or the entire basin. Barrages and lock-and-dam structures occur in estuaries and tidal rivers around the world (Beelen, 2012; McCartney et al., 1998). Tidal barrages, which are intended to prevent or limit tidal influence and intrusion of brackish water, provide new agricultural areas, freshwater supply and suitable navigation or recreational conditions (Larinier, 2002a). They also impact the migration of fishes and other animals (Larinier, 2002a; Lucas et al., 2009; Gough et al., 2012; Piper et al., 2012). Nonetheless, the impacts of engineered structures in tidal waters on fish migration are considered much less frequently than

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for freshwater dams and weirs (Giannico and Souder, 2005; Gough et al., 2012; Wright et al., 2014).

Due to their location and the highly variable water levels and discharges associated with these sites, providing traditional engineering solutions for fish passage (i.e. conventional fish passes) at tidal barrages is economically and technically demanding (Guillard and Colon, 2000; Larinier, 2002a). Furthermore, provision of conventional fishways of standard design, including at tidal-water sites, does not ensure good passage performance for targeted species (Moser et al., 2000; Nichols and Louder, 1970; Roscoe and Hinch, 2010; Smith and Hightower, 2012; Stuart and Mallen-Cooper, 1999). In fact, when navigation lock operation is managed to improve fish passage, the performance of those structures can be even better than existing fish passes (Moser et al., 2000). In addition, navigation locks can be the only available option at low-head dams (whether tidal or freshwater) for fish to pass an obstacle (Buyse et al., 2008; Johnson et al., 2005). Thus, although variable results have been obtained, previous studies suggest that, when their operation is adjusted to favour fish passage, navigation locks have the potential to be used as a cost-effective alternative for fish migration where they are present (Garrone-Neto et al., 2014; Lin et al., 2013; Lucas and Baras, 2001; Moser et al., 2000; Travade, 2002). However, information concerning the potential of navigation locks for fish passage is scarce (Garrone-Neto et al., 2014; Lin et al., 2013; Young et al., 2012) and is mainly focused on shads (Bailey et al., 2004; Ely, 2007; Guillard and Colon, 2000; Moser et al., 2000; Nichols and Louder, 1970; Smith and Hightower, 2012; Young et al., 2012).

Navigation locks in tidal and non-tidal waters have been employed as migration routes for fish using an operation protocol similar to a fish lift (i.e. Bailey et al., 2004; Guillard and Colon, 1998; Moser et al., 2000; Nichols and Louder, 1970; Young et al., 2012), but rarely if ever as a vertical slot fish pass. Those 'fish lift' protocols comprised a series of lockage cycles in which the upstream and downstream gates and valves open at different times to attract to and retain fish in the lock and subsequently to allow upstream movement. Usually the upstream gates are kept closed at the start, only opening the accessory valves to provide attraction flow. Both or one of the downstream gates are open during that period to allow fish entrance to the lock. Thereafter the downstream gates close and the upstream ones open to allow upstream migration. The availability of passage is reduced (upstream or downstream gates close) in this operation and some individuals entering the lock can leave the structure downstream before the upstream gates open to allow upstream passage (Moser et al., 2000). Thus, new approaches to operation of navigation locks, such as their use as vertical slot fish passes (partially opening the lock gates), should be evaluated to improve the use of locks as fish passage routes.

Diadromous species, which rely on migrations between fresh and marine water for lifecycle completion, are among those taxa most affected by losses in habitat connectivity (Baras and Lucas, 2001; Hall et al., 2011; Limburg and Waldman, 2009; McDowall, 1992). Indeed, as a result of habitat fragmentation and other factors such as pollution and overfishing, most diadromous species of the North Atlantic have declined dramatically in the last century (Lassalle et al., 2009; Limburg and Waldman, 2009). As a response, and with the aim of conserving socially, economically and ecologically important species (Close et al., 2002; Helfman, 2007; Limburg and Waldman, 2009), legislation requiring free passage for diadromous species migration is increasing (Brown et al., 2013; WFD, 2000). Nonetheless, the majority of remedial effort historically has focused on salmonids, and to a lesser degree on clupeids, with much less attention being given to other taxa (Noonan et al., 2012; Roscoe and Hinch 2010), especially to poor swimmers such as lampreys (Foulds and Lucas, 2013; Keefer et al., 2011; Tummers et al., 2016). Accordingly, the aim of this study was to investigate passage of European river lamprey *Lampetra fluviatilis* (hereafter referred

to as river lamprey) at a tidal barrage through measuring 1) the performance of a navigation lock used as a vertical slot fish pass to facilitate attraction and passage, 2) the attraction and passage through alternative routes (sluices).

2. Methods

2.1. Site description

The study was carried out in autumn 2015 on the lower River Derwent, at its confluence with the tidal River Ouse, at Barmby barrage, NE England (Fig. 1). The Humber river basin, of which the Ouse is one of two major catchments, is the largest drainage basin in Britain and its estuary is highly turbid (Uncles et al., 2006). Typical Secchi depths for the Ouse and Derwent rivers in the study locality are ~0.05 m and ~0.5 m respectively (M. Lucas, unpublished data). The Ouse is macrotidal (its tidal range greater than 4 m) in its lower reaches, and is weakly brackish around Barmby (Uncles et al., 2006). A variety of strictly diadromous, euryhaline and freshwater fishes exhibit seasonal movements within the tidal Ouse but are limited in their access to tributaries (Lucas et al., 1998). Parts of the Humber estuary and River Derwent are Special Areas of Conservation (EU Natura 2000 sites), for which sea lamprey *Petromyzon marinus* and river lamprey are conservation-listed features (Foulds and Lucas, 2014). Barmby barrage, which is the first obstruction for upstream-migrating fishes in the Derwent, has been shown to be a major obstacle for river lamprey migration (Lucas et al., 2009), and is presumed to significantly affect other diadromous species (Nunn and Cowx, 2012). Barmby barrage is a tidal barrage with two undershot sluice gates (7 m wide × 5 m high, with a fixed width and variable aperture height of up to 5 m) and a navigation lock (20 m long and 5 m wide, ~4 m deep at high tide; one lock chamber with steel gates) on the west side of the river (Fig. S1). The purpose of the barrage is to prevent the penetration of tidal water from the Ouse to the Derwent and to maintain suitable water levels upstream of the barrage, principally for potable water abstraction purposes.

2.2. Sluice operation

The sluice opening procedures comprise several phases, which are dependent on water levels upstream (Derwent) and downstream (Ouse) of the barrage (JBA, 2004; Fig. S2). During the Tide Lock Phase the sluices remain closed while the Ouse water level is higher than the Derwent level (most of the flooding tide and usually the first 1.5 h of the ebbing tide). The subsequent Free Flow Phase starts during the ebbing tide when the Derwent level is higher than in the Ouse. During this phase the water level in the Derwent tracks that in the Ouse and therefore is the phase that provides lower heads (difference between upstream and downstream water levels) at the barrage. The Retention Phase is activated if the water level necessary for abstraction and navigation upstream is compromised. During this phase the sluice openings are reduced, releasing a lower flow, to maintain a constant water level upstream of the barrage, instead of tracking the downstream level (moving with the tide). Retention phases are usually activated only with Derwent flows lower than 25 m s^{-3} (JBA, 2004; representing approximately an annual flow exceedance value of Q_{20}). The cycle starts again at the flooding tide when the Ouse level reaches the Derwent level, which activates the lock phase.

The tidal cycle was completed at Barmby in an average ($\pm$ SE) of $12.4 \pm 0.1 \text{ h}$ (range: 11.5–13.7 h) during the study period (24 November to 21 December 2015). The flooding and ebbing tides comprised an average of $2.8 \pm 0.1 \text{ h}$ and $9.6 \pm 0.1 \text{ h}$ per tide respectively. The tidal range was (mean $\pm$ SE) $2.8 \pm 0.1 \text{ m}$ (range: 0.8–4.4 m).

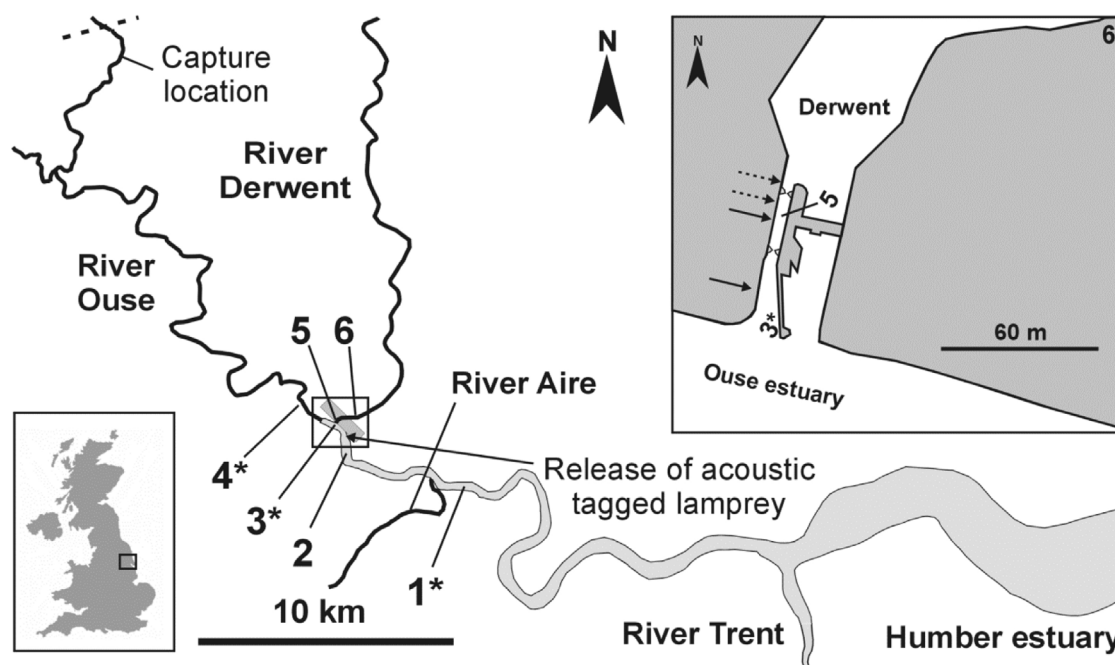


Fig 1. Map of the study area, with the estuary locality shown in the bottom left inset. Location of Barmby tidal barrage at the mouth of the River Derwent is shown as a grey bar and as a zoomed image in the top right corner (dotted arrows: position of PIT arrays; full arrows: release location of PIT and PIT + radio tagged lamprey). Numbers correspond to acoustic logging locations (*: location with two acoustic receivers; absence of asterisk indicates a single acoustic receiver). Dashed section on River Ouse denotes tidal limit at Naburn weir.

2.3. Navigation lock as a fish pass

A series of pilot studies (B. Byatt, unpublished data), developed the operation of the navigation lock at Barmby barrage as a vertical slot fish pass (formed by the vertical openings between each pair of lock gates; Fig. S3) during the main upstream river lamprey migration season (October to December; Masters et al., 2006; Foulds and Lucas, 2014) since 2007. The barrage's operational software enables the navigation lock gates to open automatically (ca. 4 h; preset opening gap of 0.4 m) five minutes before the sluice gates (to facilitate fish attraction) at the start of the ebb tide. The sluice opening procedure is set with the aim to provide head (<0.24 m, so <0.12 m per gate pair) and associated water velocities through the lock (<1.5 m s⁻¹) within the range of observed swimming speeds for lampreys (Kemp et al., 2011). The system software controlling the lock gates was set to close the gates 4 h after they first opened, or when the water level in the Derwent fell below 1.5 m, or when the water level in the Ouse was higher than the Derwent level. These settings were based on pilot study outcomes, with the aim of meeting the water regulation requirements of the barrage and providing water flow through the navigation lock, at the head constraints indicated above, while tracking the ebbing Ouse tide level, for as long a period as normally feasible.

2.4. Experimental design, lamprey capture and tagging

Individual lamprey attraction, passage efficiency and route of movement were measured using telemetry (Cooke et al., 2012). Only a small proportion of lamprey captured from, and released into, the Ouse was expected to attempt to enter the Derwent (Lucas et al., 2009), since the latter constitutes a small percentage of Ouse freshwater discharge (10.3% during this study), immediately downstream of the confluence. Due to cost (and hence sample size) constraints, several methods were combined to quantify lamprey movements. Passage efficiency through the lock was measured by Passive Integrated Transponder (PIT) telemetry of relatively large

samples of lamprey, at low cost per tag, while acoustic telemetry (high cost per tag) of smaller samples was used to measure attraction from the Ouse to the barrage and passage past the barrage, via the lock and sluices.

Lamprey were captured from the upper tidal Ouse (as capture is not feasible in the fast tidal flow area at or downstream of Barmby), using unbaited two-funnel eel pots (Masters et al., 2006), and taken to Barmby for tagging and release. This approach is valid since river lamprey in the Derwent and Ouse are the same genetic stock (Bracken et al., 2015) and, previous studies found no difference in the pattern of upstream migration of displaced river lamprey and lamprey released at the capture point; the dominant response is migration towards freshwater flow (Lucas et al., 2009).

Lamprey for tagging were anaesthetised using a buffered 0.1 g l⁻¹ solution of MS-222. Total body length (± 1 mm) and weight (± 1 g) were obtained for each individual. A total of 257 lamprey were tagged by implanting a 32 mm $\times$ 3.65 mm PIT tag (HDX, Texas Instruments model RI-TRP-RRHP, 134.2 kHz, 0.8 g in air) into the body cavity. A mid-ventral incision closed by a single suture (coated Vicryl, 4/0) was performed for this purpose under UK Home Office License following the Animal Scientific Procedures Act (1986). In addition, eight individuals were double tagged with PIT and radio tags (tag type PIP, 173 MHz, Ag 392 cell, 17 $\times$ 8.2 $\times$ 6.0 mm, potted in medical grade silicone, 1.3 g in air, with a 0.1 m $\times$ 0.1 mm whip antenna; Biotrack Ltd.). Finally, a sample of 59 lamprey were also double tagged with PIT and a coded 69 kHz acoustic transmitter (Model LP-7.3, 18 mm $\times$ 7.3 mm, 1.9 g in air, 10–30 s code interval nominal repeat, 30 days minimum tag life, Thelma Biotel AS). After acoustic or radio tagging, the incision was closed with three separate sutures. Fish were allowed to fully recover (ca. 1 h) in aerated water before release.

A randomly-selected sample of lamprey taken from the traps and used for the experiments had average length of (mean $\pm$ SE) 372 $\pm$ 1.1 mm (range: 313–444 mm) and weighed 83 $\pm$ 0.8 g (range: 48–155 g). However, only individuals with total length ≥ 379 mm were tagged with acoustic or radio tags. Average tag burden was

≤2.6% for all tag combinations with a maximum of 3.1% (Table S1). The spawning of river lamprey in this river basin takes place mainly in April and May (Jang and Lucas, 2005; Silva et al., 2015). Therefore, lamprey were tagged long before the spawning period and there was enough room in the body cavity to hold the tag.

2.5. PIT and radio telemetry

For PIT and radio + PIT tagged lamprey, releases were made into and immediately downstream of the navigation lock in 11 replicate trials or experimental events (Table S2). Each trial covered the entire period of the lock opening in fish pass mode in one tidal cycle, during which lamprey were released and tracked. Five trials were carried out during the day and six during the night (Table S2). The average ($\pm$ SE) duration of trials with PIT telemetry was 4.2 ± 0.3 h, reflecting the duration of lock opening during these tidal cycles. The sluices remained open for several hours more (average $\pm$ SE: 9.1 ± 0.2 h per tide). Twenty-five lamprey were released per trial, 10 in the mouth of the Derwent (10–12 m downstream of the lock), and 15 within the lock (10–12 m downstream of the upstream gates of the lock) (Fig. 1). In a few cases sample sizes varied, based upon fish availability. A total of 157 lamprey were released within the lock and 108 downstream of the lock. At each release point one lamprey was released at five minute intervals from the start of the trial (from when the gates opened) to minimise the likelihood of missing PIT detections caused by ‘blocking’ effects of multiple PIT tags being present within an antenna field.

A pass-through synchronised Master-Slave half-duplex (HDX) PIT detection system (Wyre Microdesign, UK) based upon the design of Tummers et al. (2016) was installed in and upstream of the navigation lock. Due to the large area to be interrogated (ca. 5 m width and ca. 4.5 m deep), and the significant amount of metal and electrical interference, it was a challenge to find an appropriate array configuration to interrogate the entire water column in and upstream of the lock. After intensive testing, the selected configuration had three loops (bottom, middle, top) per array and each array consisted of two frames separated by ~1.5 m to limit field interference (Fig. 2). One array was placed 3 m downstream and one 3 m upstream of the upstream gates of the lock (Fig. 1; Fig. S3). It was not possible to place PIT antennas immediately downstream of the navigation lock because of the large channel width, the strong currents, large floating debris and highly variable depth. All loops were made of 3.7 mm diameter, 50/0.25 mm strands, insulated tri-rated wire. The skeletons of the arrays were made mainly of 8 mm nylon yacht cord, having half a high-density breeze block as an anchor weigh and a wooden beam ca. 5 m above the channel bed (Fig. 2).

Detection ranges of at least 0.4–0.5 m were achieved for all antennas. A test tag was placed through each antenna to check that the equipment was functioning correctly before and after each trial. No holes in the detection field were found, despite repeated, intensive tests over the whole study period. The efficiency of the PIT array located within the lock was obtained by comparing the fish-borne tags detected there to those detected in the upstream array (100% efficiency would be reached if all tags detected upstream had been detected downstream). Manual radio-tracking provided evidence of detection efficiency of the upstream most PIT array and of lamprey behaviour in and around the lock.

As the PIT arrays were located in the vicinity of the upstream gates of the lock, the following parameters were calculated for lamprey passage through those gates in each trial: 1) Percentage of lamprey attempting to pass: proportion of lamprey released that passed the array located within the lock (number of lamprey detected adjusted by the PIT array efficiency). Successive attempts from the same individual were defined as visits to the PIT array within the lock with a gap of at least 5 min without detections. 2) Passage efficiency (Aarestrup et al., 2003; Cooke and Hinch, 2013):

proportion of lamprey successfully passing the gates (based on lamprey detected upstream and the PIT array efficiency) from the total attempting. 3) Proportion passing from total released: using the total number of lamprey released instead of those attempting passage. 4) Time to passage: the duration from release, or from first detection on approaching the upstream gates, to detection after exiting the navigation lock in an upstream direction. Trial 1 (25 Nov; Table S2) was not used for calculations related to detections at the PIT array within the lock, as only the PIT array upstream of the lock was operational during this. Therefore, while trial 1 was not used to calculate the percentage of lamprey attempting, passage efficiency or efficiency of the PIT array, it was used to evaluate passage and time of passage from release.

2.6. Acoustic telemetry

Coded 69 KHz acoustic transmitters and receivers (Vemco VR2, Halifax, Canada) were used to evaluate attraction to the barrage and passage by sluice and lock routes. Acoustic tagged lamprey were released in the tidal Ouse, from the left (north) bank, 300 m downstream of the Derwent mouth (Fig. 1). Releases of lamprey were spread throughout the study period (Table S2) and with an average pattern of release of 1.5 individuals at the start of the ebbing tide (when lock and sluices open) and one at the start of the flooding tide.

To track the movement of the acoustic tagged individuals in the vicinity of Barmby barrage, a set of nine omnidirectional receivers were deployed in six locations in the tidal Ouse and the Derwent (Fig. 1). The receivers were operational from 26 October 2015–3 January 2016 (acoustic tagged lamprey were released from 24 November 2015–18 December 2015). Several tests were carried out at different flow and tide conditions to determine the range of detection of the receivers (detection radius was ca. 50–100 m depending on receiver location). No test tags placed at any location downstream of the barrage could be detected by the receiver located in the Derwent upstream of the barrage.

From the acoustic receiver data the following parameters related to lamprey passage at Barmby barrage were calculated: 1) Percentage of lamprey attempting to pass: based on the time spent in the vicinity of the barrier [time continuously detected by receivers located in the Derwent mouth (location 3 in Fig. 1) without a lapse of detections greater than one hour]. 2) Passage efficiency (Aarestrup et al., 2003; Cooke and Hinch, 2013): proportion of lamprey successfully passing the barrage from the total attempting. 3) Time to passage of the barrage: from first detection at location 3 (Derwent mouth) to first detection upstream of the barrage (location 6 in Fig. 1). 4) The route by which the lamprey passed the barrier (lock or sluices) was determined, based on the pattern of detections from the acoustic receivers and the PIT arrays, and availability of each route (lock-sluices opened or closed) at the moment of passage. Similarly, the timings of arrival and passage were recorded and related to environmental conditions.

2.7. Environmental conditions

Records (values every 15 min) for sluice gate operation (gate positions), head at the barrage (difference between upstream and downstream water levels), Derwent discharge at Barmby barrage and at Buttercrambe gauging weir (40 km upstream of Barmby barrage), Ouse discharge at Skelton (49 km upstream Barmby) and at Cawood (ca. 25 km upstream Barmby; adding discharge from a tributary, the River Wharfe) were obtained from the Environment Agency, England. Flows at Buttercrambe and Skelton were related to the percentage of annual exceedance (Q_x) by using an annual flow duration curve based on historic discharge data (1973–2014) (<http://nrfa.ceh.ac.uk/data/search>). Data on the posi-

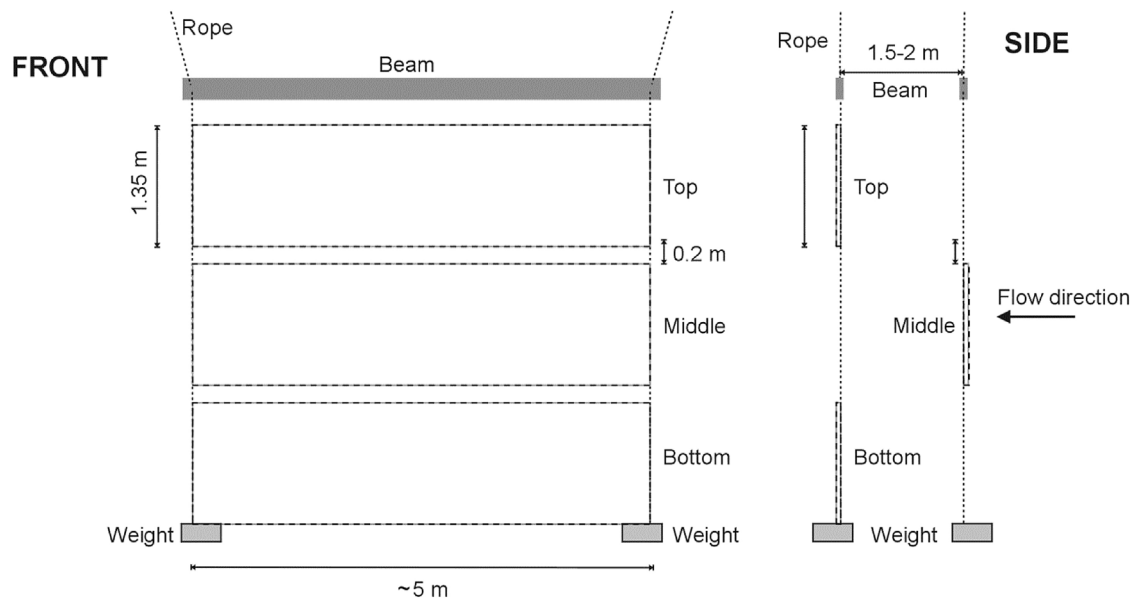


Fig. 2. Front and side views of the PIT array configuration used in this study composed of three antenna loops (top, middle and bottom).

tion of the navigation lock gates were recorded from the barrage control system display during fish release experiments at the navigation lock. Water temperatures were measured at 15 min intervals using an automatic logger (Tinytag, TG-4100) in the Derwent, 200 m upstream of Barmby barrage, and 320 m downstream in the tidal Ouse. We carried out replicate trials at the navigation lock by day ($n = 6$) and night ($n = 5$). It has been suggested that artificial light can alter the migration behaviour of lamprey (Aronsson et al., 2015); in our case throughout the experimental period barrage navigation lights remained in operation, but use of manually operated floodlights and other intense lighting forms was avoided.

Maximum estimated water flow velocity (V_{max}) in the lock (at the gates) when operating as a fish pass was obtained using the equation (Calluaud et al., 2014; Larinier, 2002b; Liu et al., 2006):

$$V_{max} = (2g \times h)^{0.5} \quad (1)$$

Where g is the acceleration due to gravity (9.81 m s^{-2}) and h is head at each drop. In this case the head calculated for the barrier is divided by two, as it was split at two points in the lock, the upstream and the downstream gates.

Discharge through the sluices (Q) was calculated as (Rajaratnam and Subramanya, 1967):

$$Q = C_d A \sqrt{2g(d_1 - 0.61b)} \text{ for free flow conditions} \quad (2)$$

and

$$Q = C_d A \sqrt{2g(d_1 - d_2)} \text{ for submerged flow conditions} \quad (3)$$

Where C_d = discharge coefficient for the gate, A = area of the aperture (height $\times$ width of the sluices opening), d_1 = upstream depth (m), b = height of the sluices opening (m) and d_2 = downstream depth (m). Following Herschy (2009) a constant C_d of 0.60 was used when the sluices were under submerged flow conditions and of 0.62 when they were under free flow conditions. Submerged or free flow conditions were determined following Swamee (1992):

$$\text{Free flow conditions: } d_1 \geq 0.81d_2(d_2/b)^{0.72} \quad (4)$$

$$\text{Submerged flow conditions: } d_1 < 0.81d_2(d_2/b)^{0.72} \quad (5)$$

Average flow velocity through the sluices was calculated as Q/A where Q is discharge through the sluices and A is the area of the aperture (height $\times$ width of the sluice opening).

When reporting environmental conditions during the study period in the text, data refer to the period from the first release of a tagged lamprey (24 Nov 2015) to the last detection of any lamprey (PIT, radio or acoustic) at the barrage (21 Dec 2015).

2.8. Data analysis

Spearman's rho (r_s), Mann Whitney (U) tests, Chi-square (χ^2) tests and logistic regressions were carried out. All analyses were performed using IBM SPSS Statistics 20.0 software.

Environmental conditions when a lamprey was passing (at first detection upstream of the barrier: upstream PIT array for PIT telemetry and receiver upstream of the barrage at location 6 for acoustic telemetry, Fig. 1) were used for investigating the effect of those conditions on the time to passage (Spearman's rho) and to compare periods (for navigation lock trials) with and without lamprey passage detected (logistic regression). For comparison of successful and unsuccessful attempts (logistic regression as well as Mann Whitney for acoustic telemetry data), environmental conditions at first detection of lamprey attempting passage (first detection within the lock for PIT study and from receivers at Derwent mouth for the acoustic study) were used. A comparison of conditions between successful vs. unsuccessful attempts at Barmby (acoustic telemetry study) was carried out for periods with accessible routes available (sluices and/or lock open). Thus, there was one lamprey attempt when the sluices were closed that was not included in the analysis because environmental conditions were evidently not the limitation for lamprey passage in that case, as there were no available routes to pass upstream. The Mann Whitney test was also used to compare the residence time at Derwent mouth between Ouse migrants and Derwent migrants. Spearman's rho was used to analyse the relation between head at the barrage and the environmental factors.

To investigate the depth of lamprey migration in the navigation lock water column (Chi-square test), the first visit of each lamprey to PIT arrays was assigned to an area of the water column (bottom, middle or top) based on the antenna loop in which the lamprey was detected (Fig. 2). When lamprey were detected at more than one antenna in the same visit, for analysis purposes this visit was assigned to the antenna in which the tag was detected most frequently. The Mann Whitney test was used to compare depth of

lamprey migration between day and night trials. The Chi-square test was also used to analyse if the frequency of acoustic tagged lamprey attempting to pass the barrage differed from the 10.3% expected, based on the average Derwent discharge during the study comprising 10.3% of the Ouse discharge, immediately downstream of the confluence, and assuming lamprey attraction proportional to freshwater discharge.

3. Results

3.1. Environmental conditions

During the period 24 November to 21 December 2015 the discharge in the Derwent was (mean $\pm$ SD) $30.9 \pm 12.6 \text{ m}^3 \text{ s}^{-1}$ (range: $2.8\text{--}52.3 \text{ m}^3 \text{ s}^{-1}$) arriving at Barmby and $30.3 (Q_{14}) \pm 7.3 \text{ m}^3 \text{ s}^{-1}$ [range: $20.2\text{--}48.2 \text{ m}^3 \text{ s}^{-1}$ ($Q_{29}\text{--}Q_4$)] at Buttercrambe. Discharge in the River Ouse was (mean $\pm$ SD) $204.8 (Q_3) \pm 86.0 \text{ m}^3 \text{ s}^{-1}$ [(range: $54.0\text{--}421.2 \text{ m}^3 \text{ s}^{-1}$ ($Q_{31}\text{--}Q_{0.1}$)] at Skelton and $270.8 \pm 116.8 \text{ m}^3 \text{ s}^{-1}$ (range: $70.7\text{--}570.9 \text{ m}^3 \text{ s}^{-1}$) at Cawood (Fig. S4). The water temperature was $7.3 \pm 1.2^\circ\text{C}$ (range: $5.1\text{--}9.8^\circ\text{C}$) in the Derwent and $6.8 \pm 1.2^\circ\text{C}$ (range: $4.6\text{--}9.5^\circ\text{C}$) in the Ouse. During the study period the percentage of Ouse discharge downstream of Barmby (Ouse discharge at Cawood + Derwent discharge at Barmby) coming from the Derwent was 10.3%.

The head at Barmby for the periods that the sluices were open was (mean $\pm$ SD) $0.12 \pm 0.09 \text{ m}$ (range: $0.00\text{--}0.78 \text{ m}$). Although the maximum head was 0.78 m , it was 0.24 m or less for 97% of the time that the sluices were open during the study period. During the PIT trials of lock passage, the head was lower still, (mean $\pm$ SD) $0.07 \pm 0.05 \text{ m}$ (range: $0.00\text{--}0.24 \text{ m}$). The barrage head was at a minimum at the start of the trials or the sluice opening period (*ca.* zero) and then progressively increased (Fig. S2). During this study, and for periods with the sluices open, the head was lower with higher Ouse discharges at Cawood ($r_s = -0.487$, $p < 0.001$) and greater with higher Derwent discharge at Barmby ($r_s = +0.235$, $p < 0.001$).

3.2. PIT and radio telemetry

3.2.1. Percentage of lamprey attempting to pass and passage efficiency at lock

The detection efficiency of the PIT array located within the lock was (mean $\pm$ SE) $90 \pm 2.6\%$. Therefore, the estimated combined detection efficiency of both PIT arrays (located within and upstream of the lock respectively) was $[1 - (0.1 \times 0.1)] \times 100 = 99\%$. This high efficiency value is supported by radio tracking data. The eight radio tagged lamprey passed through the array located within the lock and all of them were detected by the PIT equipment. In addition, three radio tagged lamprey were tracked moving upstream to the Derwent through the upstream lock gates and all were detected by the PIT array located upstream.

Radio tracking also showed that the lamprey released in the lock spent most of their time in the upstream-most half of the lock, particularly between the PIT array and the upstream gates. During this time, periods of inactivity were observed, interspersed by periods of movement. The movement was characterised by displacements in the vicinity of the upstream gates of the lock and from one side of the lock to the other. One radio tagged lamprey that passed through the lock and migrated upstream to the Derwent showed 'fallback' behaviour, moving downstream through the sluices.

The percentage of PIT tagged lamprey moving upstream and attempting to pass the upper lock gates was high during PIT trials (Table 1): 93.3% of those released in the lock. For those detected attempting to pass the upstream gates, the number of attempts per lamprey was (mean $\pm$ SE) 1.6 ± 0.08 attempts (range: 1–8). The passage efficiency at the upstream gates was 66.4% for those

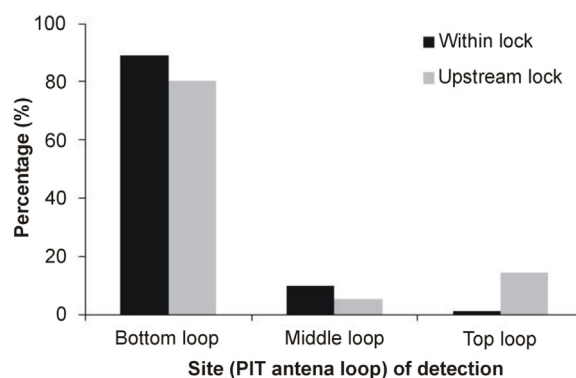


Fig. 3. Percentage of lamprey detected for the first time in each of the PIT arrays (within and upstream of the lock) grouped by the antenna loop in which they were mainly detected.

released into the lock and 78.1% for those released downstream (Table 1). Fallbacks into the lock (by those that passed upstream) were observed for five lamprey. One of those lamprey was last detected upstream of the lock.

Both within ($n = 182$; $\chi^2 = 256.0$; $d.f. = 2$; $p < 0.001$) and upstream of the lock ($n = 133$; $\chi^2 = 134.5$; $d.f. = 2$; $p < 0.001$) most lamprey were detected within the lowest third of the water column (Fig. 3). No significant differences were recorded in the percentage of lamprey detected at each loop between day and night trials (Mann Whitney U test, $p > 0.05$).

3.2.2. Environmental conditions and lamprey passage at the lock

A logistic regression analysis (69% of correct predictions) was carried out with environmental conditions at periods (of 15 min) with and without lamprey passage recorded at the lock. This analysis showed that the increase of Derwent discharge had a positive effect on lamprey passage ($B = 0.096$; Wald $\chi^2 = 19.1$; $p < 0.001$), while head at the barrage had the opposite effect ($B = -20.971$; Wald $\chi^2 = 25.5$; $p < 0.001$) (Fig. 4). Although a single lamprey passed the lock at a head of 0.24 m , 95% of individuals passed at heads $< 0.11 \text{ m}$.

For environmental conditions at successful ($n = 109$) and unsuccessful ($n = 72$) attempts, the logistic regression analysis produced a best model (64% of correct predictions) which incorporated the Derwent discharge at Barmby as a relevant variable ($B = 0.041$; Wald $\chi^2 = 8.6$; $p = 0.003$).

3.2.3. Time to passage through the lock

On average ($\pm$ SD), lamprey took $64 \pm 55 \text{ min}$ (range: $5.4\text{--}229 \text{ min}$) to pass the entire lock from the release point in the Derwent mouth; 90% did so in less than 128 min. The time to pass the upstream gates from detection immediately downstream, within the lock, was (mean $\pm$ SD) $31 \pm 45 \text{ min}$ (range: $11\text{--}238 \text{ min}$). Time to passage of the entire lock (for lamprey released downstream of the lock) was correlated with several variables recorded at the time of passage: head ($r_s = +0.734$, $p < 0.001$), maximum flow velocity through the lock ($r_s = +0.736$, $p < 0.001$), Derwent discharge at Barmby ($r_s = +0.727$, $p < 0.001$) and Ouse discharge at Cawood ($r_s = -0.422$, $p = 0.009$). Similar correlations were obtained with the time of passage of the upstream gates for the two lamprey release groups (downstream of lock and within lock) combined: head ($r_s = +0.505$, $p < 0.001$), maximum flow velocity through the lock ($r_s = +0.504$, $p < 0.001$), Derwent discharge at Barmby ($r_s = +0.477$, $p < 0.001$) and Ouse discharge at Cawood ($r_s = -0.338$, $p < 0.001$). There was no clear trend between time to passage and estimated maximum flow velocity when it is $\leq 0.5 \text{ m s}^{-1}$ (head $\leq 0.03 \text{ m}$, Fig. 5). However, the time to passage of

Table 1

Mean $\pm$ SE of the percentage of lamprey attempting to pass the upstream gates of the lock at Barmby Barrage, passage efficiency and passage from total released. Lock: lamprey released in lock; DSlock: downstream of the lock (at Derwent mouth), based upon 11 trials.

Release site	N released ^a	Lamprey attempting (%)	Passage efficiency (%)	Passage from released (%)
Lock	144	93.3 $\pm$ 2.6 (80.0–100.0)	66.4 $\pm$ 5.9 (31.8–96.4)	62.7 $\pm$ 6.7 (29.7–96.4)
DSlock	96	54.8 $\pm$ 7.3 (20.0–81.8)	78.1 $\pm$ 8.1 (31.8–100.0)	42.6 $\pm$ 7.6 (11.1–80.0)

^a Lamprey from trial 1 not used due to the absence of PIT array within the lock in that trial (PIT array only upstream of the lock).

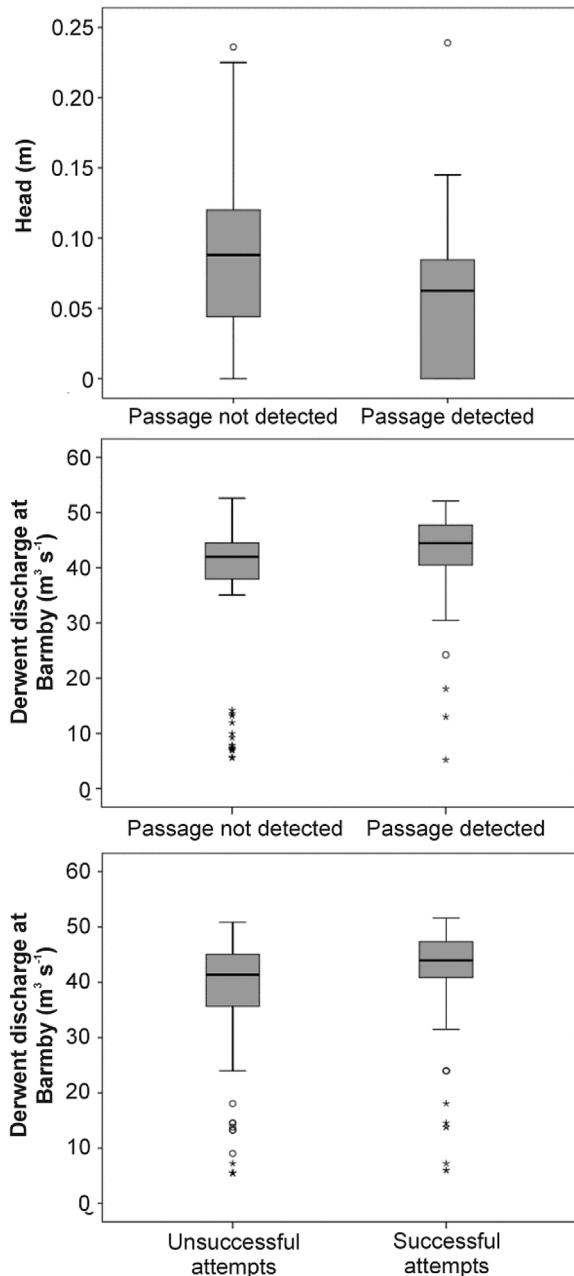


Fig. 4. Box plot (median, upper and lower quartiles, minimum and maximum and outlier values) of: head (top) and Derwent discharge at Barmby (middle) for 15 min periods (of PIT trials) with or without lamprey passage detected (by the PIT array) upstream of the lock; bottom: Derwent discharge at Barmby at the time of first detection within the lock for successful and unsuccessful lamprey attempts.

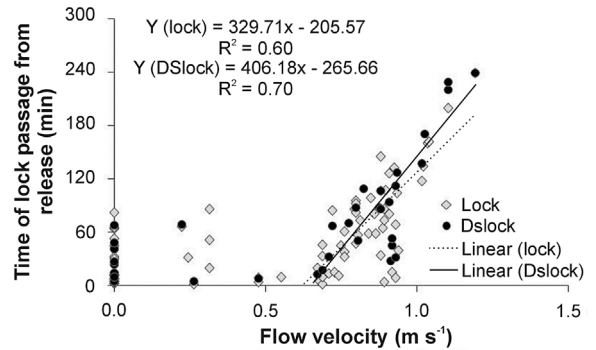


Fig. 5. Time to passage of lamprey through the navigation lock from release in the lock (lock) or downstream of it (DSlock) to first detection at the PIT array located upstream of the lock in relation to the maximum flow velocity. Trend lines made for values recorded when flow velocity was above 0.5 m s⁻¹.

the lock gates significantly increased when flow velocity (caused by an increase in head) was above those values.

3.3. Acoustic telemetry

3.3.1. Percentage of lamprey attempting to pass and passage efficiency at the barrage

Detection efficiency of acoustic receivers was (mean $\pm$ SE) 97 $\pm$ 0.7%. Only one acoustic tagged lamprey was not detected. Forty two lamprey (71%) migrated upstream through the tidal Ouse while 16 (27%) migrated to the Derwent upstream of Barmby barrage. Residence time at the Derwent confluence was significantly different for Ouse and Derwent migrants ($U = 126.0$, $p < 0.001$). Lamprey that ultimately passed the barrage spent significantly longer in the barrage outflow vicinity (detected by receivers located in the Derwent mouth), likely searching for a passage route, a mean ($\pm$ SD) of 51 $\pm$ 83 min. Five of the Ouse migrants spent an unusually long time in the Derwent confluence compared with other Ouse migrants (Fig. S5). Therefore, 36% of acoustic tagged lamprey (21 out of 59) were classed as attempting to pass the barrage, with only one attempt recorded per lamprey: passage efficiency at Barmby barrage was 76% (16 lamprey out of 21 attempting). All Derwent migrants passed the barrage at their first visit to the structure. Fifteen out of 16 lamprey passing Barmby barrage (94%) did so by the sluices. Only one lamprey passed through the lock (6%), even though the lock was open at the moment of passage for 69% of the lamprey (11 out of 16).

The percentage of lamprey attempting to pass the barrage, the passage efficiency at the barrage, and the percentage of lamprey passing the barrage from the total released, were higher for lamprey released at the start of the ebb tide than those released at the start of the flood tide (Table 2). Although lower, the number of lamprey attempting to migrate to the Derwent was not significantly different to expected values ($\chi^2 = 0.187$, $d.f. = 1$, $p = 0.665$) for lamprey released at the start of the flood tide. On the contrary, the percentage of lamprey attempting was significantly higher ($\chi^2 = 64.08$, $d.f. = 1$, $p < 0.001$) for lamprey released at the start of the ebb tide

Table 2

Lamprey attempting to pass Barmby barrage, passage efficiency and lamprey passing from the total released grouped by tidal phase of release.

Release tide	Released (n)	Attempting [n (%)]	Passing (n)	Passage efficiency (of barrage attempts) (%)	Passage efficiency (from all released) (%)
Low/early flood	24	3 (12.5%)	2	67	8
High/early ebb	35	18 (51.4%)	14	78	40

(when the sluices and lock open and there is a higher discharge). Only one lamprey attempted to pass when the sluices were closed and it was not successful

3.3.2. Environmental conditions and lamprey passage at Barmby Barrage

The logistic regression analysis based on the environmental conditions at successful ($n = 16$) vs. unsuccessful ($n = 4$) attempts at Barmby did not provide any significant model, probably due to the small sample size of unsuccessful attempts. However, Ouse ($U = 9.0$, $p = 0.030$) and Derwent ($U = 10.0$, $p = 0.038$) discharges were significantly higher for successful than for unsuccessful attempts (Fig. 6). Head was lower for successful than for unsuccessful attempts but probably because of the small sample of unsuccessful attempts and the low variation in head recorded during the study, no significant differences were found for head ($U = 12.0$, $p = 0.057$).

3.3.3. Time to passage at Barmby Barrage

Time to passage at the barrage for acoustic tagged lamprey was (mean $\pm$ SD) 1.0 ± 1.4 h (range: 0.2–5.9 h). The time to passage at Barmby barrage was significantly correlated with conditions recorded when passing the barrage (when first detected upstream of the barrier) for: head ($r_s = +0.725$, $p = 0.001$), discharge through the sluices ($r_s = -0.775$, $p < 0.001$) and estimated flow velocity through the sluices ($r_s = -0.501$, $p < 0.048$).

4. Discussion

This is the first study to have reported the use of a navigation lock as a vertical slot fish pass and shows, for river lamprey, that the method has potential. Indeed, time to passage was short and passage efficiency (60–70% at upstream gates) through the navigation lock was far higher than through unmodified conventional fish passes of three designs tested in the same river for river lamprey (0–5%; Foulds and Lucas, 2013; Tummers et al., 2016). Even the percentage of passage from total released (63 and 43% for lamprey released within and immediately downstream of the lock respectively) was relatively high. Those results are promising when compared with the average passage efficiency (21.1%) of fishways for upstream migration of non-salmonid species (Noonan et al., 2012). Similar positive results were obtained for other species like shads and striped bass *Morone saxatilis* when operating locks as fish lifts (Ely, 2007; Moser et al., 2000; Smith and Hightower, 2012; Young et al., 2012).

Lamprey released adjacent to the lock and opposite the sluices were attracted to the lock. However, acoustic tracking showed that lamprey released in the Ouse 350 m downstream of the barrage were not attracted to the lock route. In fact, attraction to the lock (5%, one out of 21 lamprey) was much lower than the attraction (43–92%) observed for other fish passes in the freshwater sections of the River Derwent (Foulds and Lucas, 2013; Tummers et al., 2016). The same problem of fish attraction to navigation locks has been recorded in other studies (Ely, 2007; Monan et al., 1970; Moser et al., 2000; Travade, 2002), as they are usually located in relatively calm areas that are more suitable for boat passage (Larinier, 1998), their availability is intermittent, and sometimes (like in this study) higher discharges are released by other routes.

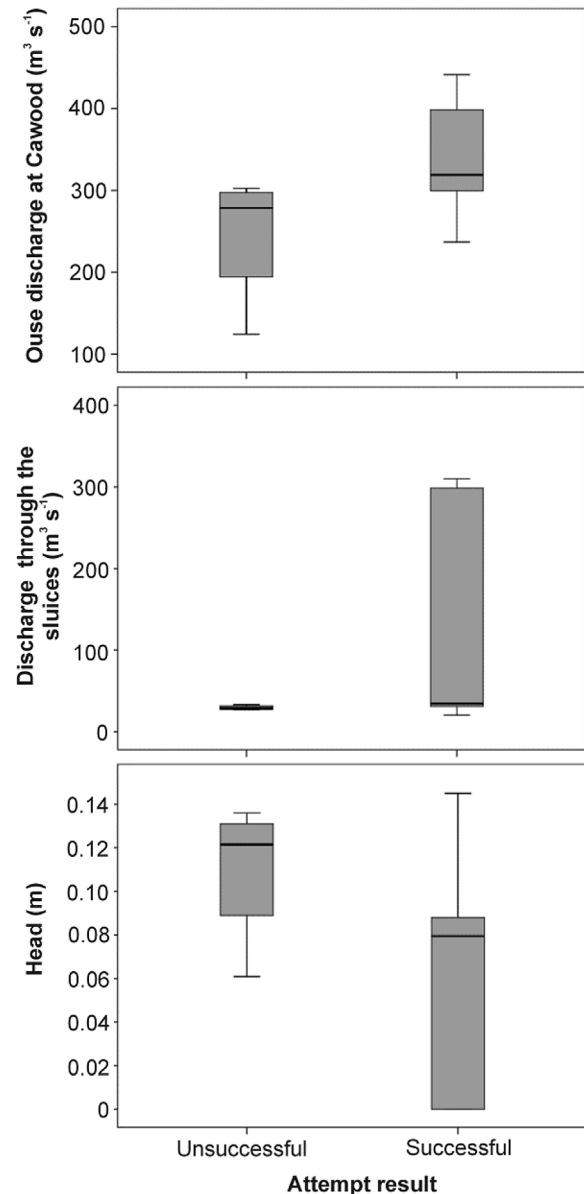


Fig. 6. Environmental conditions (median, upper and lower quartiles, minimum and maximum) at attempts of passage at Barmby barrage (at the first detection of each acoustic tagged lamprey by receivers located at the barrage outflow region). Attempts grouped by successful and unsuccessful. Only periods when the lock and/or the sluices were open were taken into account (access available at the barrier).

As shown by the acoustic telemetry data, the sluices were a suitable route for lamprey passage under the conditions present at least during part of the study period. Nonetheless, Barmby barrage is considered a significant obstacle for river lamprey migration, with lamprey passage through the sluices limited to very specific conditions (Greaves et al., 2007; Lucas et al., 2009). From a total of 77 acoustic tagged lamprey released and tracked in five con-

secutive years (2002–2007) 12 (16%) passed the barrage (Greaves et al., 2007; Lucas et al., 2009). The passage of these lamprey was restricted to five or six specific days, and at least 75% of the lamprey passed the structure at high flows (higher than $25 \text{ m}^3 \text{ s}^{-1}$, under which the retention phase of the sluices is not triggered, JBA, 2004; Section 2.2 in this study). The head at the barrage and therefore flow velocity through the lock and the sluices quickly increase during the retention phase (Fig. S2). However, due to the high flows present, the duration of retention phases was low or absent during the experimental period of this study. Thus, the head was kept at low values (under 0.24 m for 97% of the time that the sluices were open), which explains the high passage through the sluices.

As lamprey were able to pass through the barrage sluices, they did not need to search for an alternative route (the lock) to pass the obstacle. In addition, the location of the obstacle close to the confluence with the tidal Ouse can cause the 'loss' of individuals that, while initially attracted to the tributary outflow, resume migration up the main river when the conditions are not suitable for attraction or passage at the tidal barrier. That is supported by the low number of attempts at the barrage per acoustic tagged lamprey (0 or 1) and the low percentage of lamprey attempting (12.5%) and passing (8%) from those released at the flooding tide (when sluices and lock are closed; so no attraction flow nor passage route available).

During the study period the lock was only working in fish pass mode for ~30% of the time (~4 h per tide); so passage through this route was not possible for ~70% of the time. In addition, when using the lock in fish pass mode in our trials, the discharge through the lock was, on average, ~4–5% of the total. This is lower than the recommended proportion (5–10%) of river flow released through fish passes for attraction of migrating fish (Armstrong et al., 2010; Williams et al., 2012). Therefore, with the lock in fish pass mode there was a combined problem of attraction to the structure and of access availability.

Passage at tidal barriers is completely precluded when the barrage is closed to avoid water ingress upstream (tide lock phase). Under those conditions, there is neither attraction flow nor physical access available. In addition, low flow periods may limit the availability of flow to provide lamprey attraction and passage (presence of retention phase and longer tide lock phases). With low flows, lamprey passage can be prevented at the tidal barrage for long periods [more than 50% of the time (tide lock + retention phase) at Barmby barrage] and this period increases as river discharge decreases. In general, periods of low discharge will also be the most problematic in terms of lamprey passage at other obstacles (Andrade et al., 2007; Foulds and Lucas, 2013; Lucas et al., 2009; Moser et al., 2015; Tummers et al., 2016), which may generate a severe impact on lamprey recruitment. In fact, Nunn et al. (2008) recorded variable recruitment of *Lampetra ammobioetes* in the Ouse catchment, including the Derwent, especially upstream of obstacles and suggested that this may be caused by limited freshwater penetration of adult lamprey in dry years. Our studies (Foulds and Lucas, 2013; Lucas et al., 2009; Tummers et al., 2016) provide evidence that access to spawning localities by adults, rather than differences in larval mortality, may be the causal factor for the observed variability in larval recruitment. These impacts are also expected to be worse in the future, as under the current global warming scenario the low flow periods are likely to be exacerbated (van Vliet et al., 2013).

Locks (and sluices if present) operation must be adjusted at each site, within operational constraints, for optimising their effectiveness as a fish passage route (Argent and Kimmel, 2011; Moser et al., 2000; Simcox et al., 2015; Young et al., 2012). The lock must be open in fish pass mode for as long as possible. The attraction flow can be increased by leaving a larger gap between gates. The lock filling valves, as well as auxiliary water pumps, could also be used to pro-

vide or increase the attraction flow at the lock (Moser et al., 2000; Nichols and Louder, 1970; Travade, 2002; Young et al., 2012).

The necessary increase in lamprey access availability and attraction to navigation locks at tidal, or non-tidal, barriers must be achieved while keeping flow velocities in the lock that allow lamprey passage. Laboratory studies, at temperatures of ca. 12–15 °C, have shown that river lamprey can burst swim at speeds up to 2.1 m s^{-1} (Russon and Kemp, 2011). Nonetheless, river lamprey are much more successful passing velocity barriers at experimental weirs against current velocities up to 1.3 m s^{-1} than at velocities of 1.5 – 1.7 m s^{-1} (Kemp et al., 2011). These provide guidance as to the peak velocities that can be overcome, although those swimming performance studies were carried out at temperatures greater than those which river lamprey normally migrate at, and swimming performance normally declines at lower ambient temperatures (Lucas and Baras, 2001).

Recent studies suggest that lamprey can take advantage of local lower velocity areas, like wall edges or the channel bed, to pass obstacles (Keefer et al., 2011; Kemp et al., 2011; Tummers et al., 2016). For example, several (though few) lamprey were observed to have passed a gauging weir (1.3 m head, 1:2 upstream and 1:5 downstream slopes) with flow velocities of 3 m s^{-1} (Tummers et al., 2016). The most likely route at that structure was at the junction between the wing-wall and weir-face (Kemp et al., 2011; Tummers et al., 2016). Therefore, even if the flow velocity is higher than suggested ($\leq 1.3 \text{ m s}^{-1}$), it may be beneficial to keep the lock in fish pass mode, as some of the river lamprey migrants will likely be able to pass under higher flow velocity conditions and attraction is likely to be better during those conditions. Nevertheless, time to passage of Barmby navigation lock increased with head and associated flow velocity in the vertical slots, so there is an undoubted trade-off between lock flow for attraction and passage of river lamprey. The majority of radio-tracked individuals exhibited behaviour characterised by multiple lateral transitions, close to the upstream gates of the lock, likely seeking the most suitable route to move upstream.

Our use of a novel depth-stratified PIT array revealed the demersal behaviour of migrating river lamprey when passing through the navigation lock both during day and night trials. Lamprey were also observed to migrate both during day and night in the Ouse estuary during the study period, probably as a result of the turbid water conditions (Secchi depths ~0.05–0.5 m, authors' unpublished data). Although bed-orientated behaviour by river lamprey has been recorded in shallow-water flumes (Kemp et al., 2011), this is the first evidence for river lamprey in deep water. Similar behaviour was observed for landlocked sea lamprey (Holbrook et al., 2015) and Pacific lamprey *Entosphenus tridentatus* (Kirk et al., 2015). As previously stated, this behaviour of lamprey may facilitate passage at complex obstacles and could save energy during the migration.

4.1. Advantages of using navigation locks as fishways

Several advantages exist for achieving upstream fish passage via a navigation lock operated as a vertical slot fishway, in comparison with access via undershot sluices. The head at the lock is split in two 'steps' (upstream and downstream gates of the structure), providing lower average flow velocities. The slots in the lock are also separated by the boat-mooring pool, with much lower average velocity, providing a temporary resting area. Turbulence, which can have a negative impact on fish migration (Lucas and Baras, 2001), including lampreys (Kirk et al., 2016; Tummers et al., 2016), is also much lower in locks (Moser et al., 2000). Finally, the vertical slot provides passage opportunities through the entire water column. Although, as observed in this study, lampreys usually migrate close to the bottom (Holbrook et al., 2015; Keefer et al., 2011; Kemp et al., 2011; Kirk et al., 2016), the lock (cf sluices) may be a better option

for other species, such as adult Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*, which tend to migrate in the upper part of the water column. For the same reason, a lock with full water column access would be a better passage option for adult lampreys than overshot sluices (Kemp et al., 2011; Russon and Kemp, 2011). In addition, other species and life stages with low swimming performance, such as glass eel/elver *Anguilla* sp., smelt *Osmerus eperlanus*, flounder *Platichthys flesus* or cyprinid, percoid and esocid fishes, for which passage through sluices may be challenging due to the high flow velocities, may benefit from passage through navigation locks such as at Barmby.

As lamprey swimming performance is lower than for most teleost fishes (Katopodis and Gervais, 2012; Kemp et al., 2011; Kirk et al., 2015; Mesa et al., 2003), it is expected that the lock, managed in the manner described, will be passable for a wide range of species. Previous studies at Barmby barrage, using Dual Image Dual Frequency Identification Sonar (DIDSON), recorded passage through the lock (in fish pass mode) of several species and in different directions (B. Byatt, unpublished data). Anadromous salmonids (*Salmo* sp.), pike *Esox lucius* and adult river lamprey were identified passing in an upstream direction, while individuals considered to be recently transformed lamprey, adult eel *Anguilla anguilla* and cyprinid fish were observed moving downstream (B. Byatt unpublished data). Therefore, locks may also provide suitable routes for downstream migration. In fact, different studies showed that a wide variety of fish including migratory and resident species (Chondrichthyes and Osteichthyes, comprising anguilliform, flattened and fusiform morphotypes) can pass through navigation locks used for boat passage (Argent and Kimmel, 2011; Caswell, 2010; Hartman et al., 2000; Johnson et al., 2005; Lin et al., 2013; Margraf and Knight, 2002; Monan et al., 1970; Pegg et al., 1997; Piper et al., 2013; Winter et al., 2014). However, there is an important lack of knowledge on the effectiveness of using navigation locks with modified management to facilitate passage, as most of the few existent studies have been focussed on using locks as fish lifts for shad migration (Bailey et al., 2004; Guillard and Colon, 2000; Moser et al., 2000; Nichols and Louder, 1970; Young et al., 2012).

The availability of passage through locks when used as a fish lift is reduced (upstream or downstream gates close) and some individuals can leave the structure before the upstream gates open to allow upstream passage (Moser et al., 2000). In contrast, as a vertical slot fish pass, navigation locks can have a more continuous passage availability. Nonetheless, the “fish lift” operation procedure is suitable to be used with high heads, as is common case in non-tidal areas. Thus, using different approaches locks can provide fish passage under different conditions and in different habitats. Currently there are more than 15000 km of navigable rivers and estuaries in Europe (Beelen, 2012) and more than 40000 km in USA (McCartney et al., 1998) supported by the existence of an important set of lock-and-dam structures. There are also relevant inland navigation corridors in South America and Asia, especially in Brazil and China, and in some African countries (Beelen, 2012). Therefore, there is a clear potential worldwide to increase the habitat availability and recruitment of fishes by using navigation locks as fishways. Consequently, management of barrage or lock-and-dam structures should be adjusted to provide fish passage wherever possible. Even if the passage performance may be low, depending on the species and the environmental conditions, the positive impact on fish populations may be high, based on the key location of lock-and-dam structures (lower river reaches and estuaries). Accordingly, Pereira et al. (2016), observed that the recent installation of a vertical slot fish pass in River Mondego provided a rapid colonization and an important recruitment increase of the sea lamprey *P. marinus* in the river section located upstream of the obstacle, even with a relatively low passage efficiency (31%). Besides, using

locks for fish passage is a much more cost effective option than the construction of fish passes (Moser et al., 2000), that might even perform worse than navigation locks (Nichols and Louder, 1970; Moser et al., 2000; Smith and Hightower, 2012; Stuart and Mallen-Cooper, 1999).

In conclusion, this study shows that navigation locks at tidal barrages have the potential to be used as a route for lamprey migration. Further studies are encouraged to evaluate the effectiveness of the actual and modified navigation lock operation protocols under different environmental-habitat conditions and for a wide range of species. Special attention must be paid to maximize the period of opening (access availability) and the attraction (appropriate flow through the lock; utility of using accessory gates, pumps and greater gate opening), while keeping flow velocities through the structure sufficiently low ($<1.3 \text{ m s}^{-1}$ when possible for river lamprey). Adaptive management of those structures should be based on the evidence of fish passage, not assumptions, in order to optimize their effectiveness. Local characteristics at each site have to be taken into account as they may require specific management to maximize passage efficiency. Future studies on the medium-long term effect of using locks as fish passes, including on fish community structure and population dynamics, are also desirable.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecoleng.2017.02.027>.

References

- Aarestrup, K., Lucas, M.C., Hansen, J.A., 2003. Efficiency of a nature-like bypass channel for sea trout (*Salmo trutta*) ascending a small Danish stream studied by PIT telemetry. *Ecol. Freshw. Fish* 12, 160–168.
- Andrade, N.O., Quintella, B.R., Ferreira, J., Pinela, S., Póvoa, I., Pedro, S., Almeida, P.R., 2007. Sea lamprey (*Petromyzon marinus* L.) spawning migration in the Vouga river basin (Portugal): poaching impact, preferential resting sites and spawning grounds. *Hydrobiologia* 582, 121–132.
- Argent, D.G., Kimmel, W.G., 2011. Influence of navigational lock and dam structures on adjacent fish communities in a major river system. *River Res. Appl.* 27, 1325–1333.
- Armstrong, G.S., Aprahamian, M.W., Fewings, G.A., Gough, P.J., Reader, N.A., Varallo, P.V., 2010. Environment Agency Fish Pass Manual: Guidance Notes on the Legislation, Selection and Approval of Fish Passes in England and Wales. Environment Agency, Rio House, Bristol <http://publications.environment-agency.gov.uk>.
- Aronson, K., Marjomäki, T.J., Tuohino, J., Wennman, K., Vikström, R., Ojutkangas, E., 2015. Migratory behaviour and holding habitats of adult river lampreys (*Lampetra fluviatilis*) in two Finnish rivers. *Boreal Environ. Res.* 20, 120–144.
- Bailey, M.M., Isely, J.J., Bridges Jr., W.C., 2004. Movement and population size of American shad near a low-head lock and dam. *Trans. Am. Fish. Soc.* 133, 300–308.
- Baras, E., Lucas, M.C., 2001. Impacts of man's modification of river hydrology on freshwater fish migration: a mechanistic perspective. *Ecohydrol. Hydrobiol.* 1, 291–304.
- Beelen, M., 2012. Structuring and Modelling Decision Making in the Inland Navigation Sector. Ph.D. Universiteit Antwerpen.
- Bracken, F.S., Hoelzel, A.R., Hume, J.B., Lucas, M.C., 2015. Contrasting population genetic structure among freshwater-resident and anadromous lampreys: the role of demographic history, differential dispersal and anthropogenic barriers to movement. *Mol. Ecol.* 24, 1188–1204.

- Brown, J.J., Limburg, K.E., Waldman, J.R., Stephenson, K., Glenn, E.P., Juanes, F., Jordaan, A., 2013. Fish and hydropower on the US Atlantic coast: failed fisheries policies from half-way technologies. *Conserv. Lett.* 6, 280–286.
- Buysse, D., Coeck, J., Maes, J., 2008. Potential re-establishment of diadromous fish species in the River Scheldt (Belgium). *Hydrobiologia* 602, 155–159.
- Calluad, D., Pineau, G., Texier, A., David, L., 2014. Modification of vertical slot fishway flow with a supplementary cylinder. *J. Hydraul. Res.* 52, 614–629.
- Caswell, N.M. (Ed.), 2010. U.S. Army Corps of Engineers, Rock Island, St. Louis, and St. Paul Districts.
- Close, D.A., Fitzpatrick, M.S., Li, H.W., 2002. The ecological and cultural importance of a species at risk of extinction, Pacific lamprey. *Fisheries* 27, 19–25.
- Cooke, S.J., Hinch, S.G., 2013. Improving the reliability of fishway attraction and passage efficiency estimates to inform fishway engineering science, and practice. *Ecol. Eng.* 58, 123–132.
- Cooke, S.J., Hinch, S., Lucas, M.C., Lutcavage, M., 2012. Biotelemetry and biologging. In: Zale, A., Parrish, D., Sutton, T. (Eds.), *Fisheries Techniques*, 3rd ed. American Fisheries Society, Bethesda, Maryland, pp. 819–881.
- Ely, P., 2007. Population Size and Passage Efficiency of Alabama Shad Reaching Jim Woodruff Lock and Dam. Master Thesis. Clemson University.
- Foulds, W.L., Lucas, M.C., 2013. Extreme inefficiency of two conventional, technical fishways used by European river lamprey (*Lampetra fluviatilis*). *Ecol. Eng.* 58, 423–433.
- Foulds, W.L., Lucas, M.C., 2014. Paradoxical exploitation of protected fishes as bait for anglers: evaluating the lamprey bait market in Europe and developing sustainable and ethical solutions. *PLoS One* 9 (6), e99617.
- Garrone-Neto, D., Haddad Jr., V., Gadig, O.B.F., 2014. Record of ascending passage of potamotrygonid stingrays through navigation locks: implications for the management of non-native species in the Upper Paraná River basin, southeastern Brazil. *Manag. Biol. Invasions* 5, 113–119.
- Giannico, G., Souder, J.A., 2005. Tide Gates in the Pacific Northwest: Operation, Types and Environmental Effects. Oregon state University, Oregon.
- Gough, P., Philipsen, P., Schollemma, P.P., Wanningsen, H. (Eds.), 2012. *Regional Water Authority Hunze en Aas, AD Veendam, The Netherlands*.
- Greaves, R.K., Bubbs, D.M., Lucas, M.C., 2007. Adult River Lamprey Occurrence and Migration in the River Trent in Relation to Barriers and Environmental Conditions, 2006–2007. Final Report.
- Guillard, J., Colon, B., 1998. Estimation hydroacoustique du nombre de poissons migrateurs franchissant l'écluse de Beaucaire-Vallabrègues (Rhône). *Bull. Fr. Peche Piscic.* 348, 79–90.
- Guillard, J., Colon, M., 2000. First results on migrating shad (*Alosa fallax*) and mullet (*Mugil cephalus*) echocounting in a lock on the Rhône River (France) using a split-beam sonar, and relationships with environmental data and fish caught. *Aquat. Living Resour.* 13, 327–330.
- Hall, C.J., Jordaan, A., Frisk, M.G., 2011. The historic influence of dams on diadromous fish habitat with a focus on river herring and hydrologic longitudinal connectivity. *Landsc. Ecol.* 26, 95–107.
- Hartman, K.J., Nagy, B., Tipton, R.C., Morrison, S., 2000. Verification of hydroacoustic estimates of fish abundance in Ohio River lock chambers. *N. Am. J. Fish. Manag.* 20, 1049–1056.
- Helfman, G.S., 2007. *Fish Conservation. A Guide to Understanding and Restoring Global Aquatic Biodiversity and Fishery Resource*. Island Press, Washington, USA.
- Hersch, R.W., 2009. *Streamflow Measurement*, third edition. Routledge, Taylor and Francis group, London.
- Holbrook, C.M., Bergstedt, R., Adams, N.S., Hatton, T.W., McLaughlin, R.L., 2015. Fine-scale pathways used by adult Sea lampreys during riverine spawning migrations. *Am. Fish. Soc.* 144, 549–562.
- JBA, 2004. Impact of the Barmby Barrage on the Lower Derwent and Derwent Ings. Final Report. Environment Agency.
- Jang, M.H., Lucas, M.C., 2005. Reproductive ecology of the river lamprey. *J. Fish Biol.* 66, 499–512.
- Johnson, P.N., Bouchard, K., Goetz, F.A., 2005. Effectiveness of strobe lights for reducing juvenile salmonid entrainment into a navigation lock. *N. Am. J. Fish. Manag.* 25, 491–501.
- Katopodis, C., Gervais, R., 2012. Ecohydraulic analysis of fish fatigue data. *River Res. Appl.* 28, 444–456.
- Keefer, M.L., Peery, C.A., Lee, S.R., Daigle, W.R., Johnson, E.L., Moser, M.L., 2011. Behaviour of adult Pacific lamprey in near-field flow and fishway design experiments. *Fish. Manag. Ecol.* 18, 177–189.
- Kemp, P.S., O'Hanley, J.R., 2010. Procedures for evaluating and prioritising the removal of fish passage barriers: a synthesis. *Fish. Manag. Ecol.* 17, 297–322.
- Kemp, P.S., Russon, I.J., Vowles, A.S., Lucas, M.C., 2011. The influence of discharge and temperature on the ability of upstream migrant adult river lamprey (*Lampetra fluviatilis*) to pass experimental overshoot and undershot weirs. *River Res. App.* 27, 488–498.
- Kirk, M.A., Caudill, C.C., Johnson, E.L., Keefer, M.L., Clabough, T.S., 2015. Characterization of adult Pacific lamprey swimming behavior in relation to environmental conditions within large-dam fishways. *Am. Fish. Soc.* 144, 998–1012.
- Kirk, M.A., Caudill, C.C., Tonina, D., Syms, J.C., 2016. Effects of water velocity, turbulence and obstacle length on the swimming capabilities of adult Pacific lamprey. *Fish. Manag. Ecol.* 23, 356–366.
- Larinier, M., 1998. Upstream and downstream fish passage experience in France. In: Jungwirth, M., Schmutz, S., Weiss, S. (Eds.), *Fish Migration and Fish Bypasses*. Fishing News Books. Blackwell Science, London, pp. 127–145.
- Larinier, M., 2002a. Fish passage through culverts, rock weirs and estuarine obstructions. *Bull. Fr. Peche Piscic.* 364, 119–134.
- Larinier, M., 2002b. Pool fishways, pre-barrages and natural bypass channels. *Bull. Fr. Peche Piscic.* 364, 54–82.
- Lassalle, G., Crouzet, P., Rochard, E., 2009. Modelling the current distribution of European diadromous fishes: an approach integrating regional anthropogenic pressures. *Freshw. Biol.* 54, 587–606.
- Limburg, K.E., Waldman, J.R., 2009. Dramatic declines in North Atlantic diadromous fishes. *Bioscience* 59, 955–965.
- Lin, P.C., Brosse, S., Gao, X., Liu, C.C., Liu, H.Z., 2013. Species composition and temporal pattern of fish passing through the navigation locks in the middle reach of Yangtze River: implications for fish conservation. *J. Appl. Ichthyol.* 29, 1441–1444.
- Liu, M., Rajaratnam, N., Zhu, D.Z., 2006. Mean flow and turbulence structure in vertical slot fishways. *J. Hydraul. Eng.* 132, 765–777.
- Lucas, M.C., Baras, E., 2001. *Migration of Freshwater Fishes*. Blackwell Science, Oxford.
- Lucas, M.C., Mercer, T., Batley, E., Frear, P.A., Peirson, G., Duncan, A., Kubecka, J., 1998. Spatio temporal variations in the distribution and abundance of fishes in the Yorkshire Ouse system. *Sci. Total Environ.* 200/201, 243–257.
- Lucas, M.C., Bubbs, D.H., Jang, M.H., Ha, K., Masters, J.E., 2009. Availability of and access to critical habitats in regulated rivers: effects of low-head barriers on threatened lampreys. *Freshw. Biol.* 54, 621–634.
- Margraf, F.J., Knight, C.T., 2002. Evaluation of fish sampling using rotenone in a navigation lock. *Fish. Res.* 55, 297–305.
- Masters, J.E., Jang, M.H., Ha, K., Bird, P.D., Frear, P.A., Lucas, M.C., 2006. The commercial exploitation of a protected anadromous species, the river lamprey (*Lampetra fluviatilis* (L.)), in the tidal River Ouse, north-east England. *Aquat. Conserv.* 16, 77–92.
- McCartney, B.L., George, J., Lee, B.K., Lindgren, M., Neilson, F., 1998. *Inland Navigation: Locks, Dams, and Channels*. American Society of Civil Engineers.
- McDowall, R.M., 1992. Particular problems for the conservation of diadromous fish. *Aquat. Conserv.* 2, 351–355.
- Mesa, M.G., Bayer, J.M., Seelye, J.G., 2003. Swimming performance and physiological responses to exhaustive exercise in radio-tagged and untagged Pacific lampreys. *Am. Fish. Soc.* 132, 483–492.
- Monan, G.E., Smith, J.R., Liscom, K.L., Johnson, J.H., 1970. Evaluation of Upstream Passage of Adult Salmonids Through the Navigation Lock at Bonneville Dam During the Summer of 1969. Final Report.
- Moser, M.L., Darazsdi, A.M., Hall, J.R., 2000. Improving passage efficiency of adult American shad at low-elevation dams with navigation locks. *N. Am. J. Fish. Manag.* 20, 376–385.
- Moser, M.L., Almeida, P.R., Kemp, P.S., Sorensen, P.W., 2015. Lamprey spawning migration. In: Docker, M. (Ed.), *Lampreys: Biology, Conservation and Control*, vol 1. Springer, Dordrecht, pp. 215–252.
- Nichols, P.R., Louder, D.E., 1970. Upstream Passage of Anadromous Fish Through Navigation Locks and Use of the Stream for Nursery and Spawning Habitat, Cape Fear River, North Carolina, 1962–1966. US Fish and Wildlife Service Circular, pp. 352.
- Nilsson, C., Reidy, C.A., Dynesius, M., Revenga, C., 2005. Fragmentation and flow regulation of the world's large river systems. *Science* 308, 405–408.
- Noonan, M.J., Grant, J.W., Jackson, C.D., 2012. A quantitative assessment of fish passage efficiency. *Fish.* 13, 450–464.
- Nunn, A.D., Cowx, I.G., 2012. Restoring river connectivity: prioritizing passage improvements for diadromous fishes and lampreys. *Ambio* 41, 402–409.
- Nunn, A.D., Harvey, J.P., Noble, R.A.A., Cowx, I.G., 2008. Condition assessment of lamprey populations in the Yorkshire Ouse catchment, north-east England, and the potential influence of physical migration barriers. *Aquat. Conserv.* 18, 175–189.
- Pegg, M.A., Bettoli, P.W., Layzer, J.B., 1997. Movement of saugers in the lower Tennessee River determined by radio telemetry, and implications for management. *N. Am. J. Fish. Manag.* 17, 763–768.
- Pereira, E., Quintella, B.R., Mateus, C.S., Alexandre, C.M., Belo, A.F., Telhado, A., Quadrado, M.F., Almeida, P.R., 2016. Performance of a vertical-slot fish pass for the sea lamprey *Petromyzon marinus* L. and habitat recolonization. *River Res. Appl.*, <http://dx.doi.org/10.1002/rra.3054>.
- Pimm, S.L., Raven, P., 2000. Biodiversity: extinction by numbers. *Nature* 403, 843–845.
- Piper, A.T., Wright, R.M., Kemp, P.S., 2012. The influence of attraction flow on upstream passage of European eel (*Anguilla anguilla*) at intertidal barriers. *Ecol. Eng.* 44, 329–336.
- Piper, A.T., Wright, R.M., Walker, A.M., Kemp, P.S., 2013. Escapement, route choice, barrier passage and entrainment of seaward migrating European eel *Anguilla anguilla*, within a highly regulated lowland river. *Ecol. Eng.* 57, 88–96.
- Rajaratnam, N., Subramanya, K., 1967. Flow equation for the sluice gate. *J. Irrig. Drain. Eng.* 93, 167–186.
- Roscoe, D.W., Hinch, S.G., 2010. Effectiveness monitoring of fish passage facilities: historical trends, geographic patterns and future directions. *Fish. Fish.* 11, 12–33.
- Russon, I.J., Kemp, P.S., 2011. Experimental quantification of the swimming performance and behaviour of spawning run river lamprey *Lampetra fluviatilis* and European eel *Anguilla anguilla*. *J. Fish Biol.* 78, 1965–1975.
- Silva, S., Gooderham, A., Forty, M., Morland, B., Lucas, M.C., 2015. Egg drift and hatching success in European river lamprey *Lampetra fluviatilis*: is egg deposition in gravel vital to spawning success? *Aquat. Conserv.* 25, 534–543.

- Simcox, B.L., DeVries, D.R., Wright, R.A., 2015. [Migratory characteristics and passage of paddlefish at two Southeastern US lock-and-dam systems](#). *Am. Fish. Soc.* 144, 456–466.
- Smith, J.A., Hightower, J.E., 2012. [Effect of low-head lock-and-dam structures on migration and spawning of American shad and striped bass in the Cape Fear River, North Carolina](#). *Am. Fish. Soc.* 141, 402–413.
- Stuart, I.G., Mallen-Cooper, M., 1999. [An assessment of the effectiveness of a vertical-slot fishway for non-salmonid fish at a tidal barrier on a large tropical/subtropical river](#). *Regul. Rivers Res. Manag.* 15, 575–590.
- Swamee, P.K., 1992. [Sluice-gate discharge equations](#). *J. Irrig. Drain. Eng.* 118, 56–60.
- Travade, F., 2002. [Franchissement des barrages de navigation par les poissons](#). Possibilité d'utilisation des écluses de navigation. Technical report, Available at http://www.eau-mer-fleuves.cerema.fr/IMG/pdf/NR_31_cle22f471.pdf.
- Tummers, J.S., Winter, E., Silva, S., O'Brien, P., Jang, M.H., Lucas, M.C., 2016. [Evaluating the effectiveness of a Larinier super active baffle fish pass for European river lamprey *Lampetra fluviatilis* before and after modification with wall-mounted studded tiles](#). *Ecol. Eng.* 91, 183–194.
- Uncles, R.J., Stephens, J.A., Law, D.J., 2006. [Turbidity maximum in the macrotidal, highly turbid Humber Estuary, UK : Flocs, fluid mud, stationary suspensions and tidal bores](#). *Estuar. Coast. Shelf Sci.* 67, 30–53.
- WFD, 2000. Directive 2000/60/EC of the European Parliament and of the Council Establishing a Framework for the Community Action in the Field of Water Policy.
- Williams, J.G., Armstrong, G., Katopodis, C., Larinier, M., Travade, F., 2012. [Thinking like a fish: a key ingredient for development of effective fish passage facilities at river obstructions](#). *River Res. App.* 28, 407–417.
- Winter, H.V., Griffioen, A.B., van Keeken, O.A., 2014. [De Vismigratierivier: Bronnenonderzoek naar gedrag van vis rond zoet-zout overgangen \(No C035/14\)](#). IMARES.
- Wright, G.V., Wright, R.M., Kemp, P.S., 2014. [Impact of tide gates on the migration of juvenile sea trout, *Salmo trutta*](#). *Ecol. Eng.* 71, 615–622.
- Young, S.P., Ingram, T.R., Tannehill, J.E., Isely, J.J., 2012. [Passage of spawning alabama shad at Jim Woodruff lock and dam, Apalachicola river, Florida](#). *Am. Fish. Soc.* 141, 881–889.
- van Vliet, M.T., Franssen, W.H., Yearsley, J.R., Ludwig, F., Haddeland, I., Lettenmaier, D.P., Kabat, P., 2013. [Global river discharge and water temperature under climate change](#). *Glob. Environ. Change* 23, 450–464.